

On the Other Hand: Current Issues in and Meta-Analysis of the Behavioral Laterality of Hand Function in Nonhuman Primates

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ABSTRACT The last decade has seen a resurgence of interest in laterality of function in primates, especially in hand use as it links to handedness and language in *Homo sapiens*. Manual lateralization of behavior in humans reflects asymmetry in cerebral structure, which must have evolved from nonhuman progenitors. To what extent is hand function lateralized in our nearest living relations? First, we address current issues of theory and methodology: statistics, measurement, variables, setting, sensory modality, and sample size. Specific topics include preference vs. performance, posture, bimanuality, inheritance, and arm asymmetry. We categorize the published literature in a descriptive, classificatory framework of five levels that range from Level 1, ambilaterality, to Level 5, human-like handedness. In a meta-analysis we put 241 published data-sets to a methodological test of seven criteria and code the 48 survivors onto the levels framework, by taxonomic grouping (prosimian, New World monkey, Old World monkey, ape, chimpanzee). Primates at Level 1 are mostly wild or naturalistic populations performing spontaneous species-typical behavior patterns. Most primates are at Levels 2 and 3, that is, individually lateralized to either side, especially on complex, demanding or practiced tasks, usually as devised in captive settings. Only chimpanzees show signs of population-level bias (Levels 4 and 5) to the right, but only in captivity and only incompletely. We conclude that nonhuman primate hand function has not been shown to be lateralized at the species level—it is not the norm for any species, task, or setting, and so offers no easy model for the evolution of human handedness. *Yrbk Phys Anthropol* 40:201–232, 1997. © 1997 Wiley-Liss, Inc.

Why should any organism be asymmetrical? More to the point, why should any primate use its left hand differently from its right? In a largely symmetrical world in which predators, prey, competitors, etc., are just as likely to come from one side as the other, a mobile organism can always reposition or reorient itself and so retain the flexibility of using either or both of paired organs to act or to react. To put it another way round, why should any primate constrain its manipulatory options by biasing its manual functions? This is the basic evolu-

tionary question underlying all others, and the existence of any departure from symmetry suggests that notable benefits must be gained via natural selection if it favors such a handicap. Alternatively, lateralized hand function may be merely a by-product of some other lateralized functioning, say, of the central nervous system, selected for on other grounds (Bradshaw and Rogers, 1993).

The aim of this paper is to ask whether or not nonhuman primates show laterality of hand function, and if so, how and to what extent, and finally, if possible, why?

At the outset, it should also be made clear what this paper does not aim to do: It does not cover other sagittally paired organs, so that eyedness, earedness, nostriledness, toothedness, breastedness, gonadedness, even footedness, are omitted. Some of these have been dealt with, occasionally in relation to hand function (Cole, 1957; Hall and Mayer, 1966; Hook-Costigan and Rogers, 1995, 1998; Rogers et al., 1994), but the literature is sparse. There is more published material on hands than on all other paired organs combined.

Also, this paper says nothing about laterality of function of unpaired organs (tail, tongue, head, mouth, etc., e.g. Hauser, 1993; Rogers et al., 1993; Hopkins and Bard, 1995) or of whole organisms, as in rotation (Dodson et al., 1992; Roney and King, 1993; Westergaard and Suomi, 1996c) or orientation (Casperd and Dunbar, 1996). Doubtless these are related topics, if for no other reason than the sharing of a common cerebral substrate, but space is too limited to develop them here (see Ward and Hopkins, 1993).

For similar reasons, this paper restricts itself to nonhuman primates, however fascinating is the published literature on other orders of mammals (e.g. Collins, 1975) or on other vertebrate classes (Bisazza et al., 1996; Harris, 1989). These taxa deserve scrutiny in their own right. Similarly, we eschew *Homo sapiens*, except when this anomalous species of primate is needed as a reference point, usually as an outlier. In the process, we ignore all extinct forms: hominid, hominoid, anthropoid, etc., both paleontologically and archaeologically, even when the results or products of past behavior purport to give us data on long gone laterality. (For synthesis, see Corballis, 1989; Bradshaw and Rogers, 1993; Falk, 1980, 1987.)

Most contrivedly, this paper concerns itself with observable (behavioral) function rather than neural structure; thus we avoid neuroanatomy, neurophysiology, and much of neuropsychology. We are behavioral scientists (specifically, ethologists) trained to study whole, intact organisms, and do not pretend to be neuroscientists. We assume that brain and behavior are inseparable, but that elements of the complex can be studied

separately. If behavior is the way that brains interact with the world, then we choose to focus on this interaction (function).

Finally, this paper draws upon published books, chapters, and journal articles. It avoids popular pieces, conference presentations, unpublished manuscripts, personal communications, abstracts, theses and dissertations, etc., unless absolutely necessary, on the grounds that such knowledge is incomplete or not in the public domain. However, we acknowledge with apologies an English-language bias, which reflects our linguistic limitations, not the quality of other research.

What remains to be covered here is a corpus of more than 230 sources, from which unfolds: theoretical background, abiding issues of statistics, measurement and other aspects of methodology, special topics of current interest, a framework for categorizing results, taxonomic treatment of current knowledge, and tentative conclusions.

THEORY OF LATERALITY

Strictly speaking, there is no theory of laterality of behavioral or neural function, in the sense that there is attachment theory to explain parent-offspring relations (Bowlby, 1979) or optimal foraging theory to explain feeding (Krebs and Davies, 1997). That is, there is no inclusive formulation for why primates might be biased to one side or another, either as individuals or as populations. Instead, there are "models" of varying power.

MacNeilage et al.'s (1987; see also MacNeilage, 1991) "postural origins theory" is by far the most ambitious and comprehensive such framework. They started with an ancestral, arboreal primate that of necessity used one hand (the right) more powerfully than the other in positional and locomotor behavior. By default, this left the other hand available for visually guided reaching and grasping, especially in predation. Later, with increasing terrestriality and opportunity for bimanual activities, especially skillful object manipulation, the right hand was preadapted as a "versatile gripping device" and so was co-opted accordingly. From this emerged a generalized right-sided bias for all hand use, as shown most clearly in

human beings. From the outset, MacNeilage et al. (1987, 1988, 1991) have invited empirical testing and critical appraisal of their ideas, and more recently have sought to incorporate cerebral asymmetry and language function into a grander framework (MacNeilage, 1991, 1993). MacNeilage et al.'s challenging assertions have done more than anything else to reawaken interest in primate laterality over the last decade.

However impressive, MacNeilage et al.'s model leaves three basic questions unanswered: Why should the manual division of labor have been visuo-spatial-left hand vs. manipulative-right hand instead of vice-versa? Why should primates be a special case among arboreal or manipulative mammals? Why should such lateralized adaptations occur on a species-level, rather than individually? Apart from these still-to-be resolved points, on the general issue of whether or not primates show lateralized hand function, MacNeilage et al. (1991) are clear: They do.

The opposite viewpoint was emphatically reiterated by Warren (1977, 1980, 1987): Lateralization of hand use in primates is wholly ontogenetic, that is, learned over a course of lifetime experiences, and is thus task- and situation-specific. Essentially, this means that individual primates remain unlateralized tabula rasa in their behavioral output unless they are shaped otherwise by environmental forces. Methodology is the key to understanding the conflicting data: "...the appearance of handedness [sic] in monkeys is an artifact produced by the methods that have been used in chronic experiments" (Warren, 1980, p. 354). By this is meant that protocols calling for thousands of repetitive, stereotyped trials result in automatic, overpracticed responses. Depending on reinforcement schedules, the result may be individuals who respond ambilaterally or laterally (that is, hand preference or hand specialization, see section on principles of laterality) but show no population-level laterality (that is, task specialization or handedness) unless the salient features of the environment are skewed to produce equal effects on each individual in the population. In effect, Warren's viewpoint holds to the conservative

null hypothesis of no intrinsic differences across the sagittal plane.

Warren's viewpoint makes hemispheric asymmetry and laterality of function in *Homo sapiens* a special case among primates and other organisms. It is easily tested in the gross sense: A naive but still lateralized population will falsify his null hypothesis. More specifically, concordances of laterality across different tasks or different sets of bilateral organs, or correspondences between hemispheric asymmetries and contralateral hand functions, will likewise count against his model. A priori, it is hard to reconcile long-known asymmetries in the neural structure of nonhuman primates with the assertion of no difference in their function (Falk, 1987).

Fagot and Vauclair (1991) found a way through the horns of the dilemma by dividing hand function into two types: low-level and high-level tasks. Low-level tasks comprise grossly regulated, familiar, practiced, simple activities requiring undemanding cognitive processes. At the population level, subjects are expected to be symmetrically distributed, with just as many favoring (or failing to favor) the right hand as the left. Examples of low-level tasks are the routine acts of daily life, especially reaching for food. This, they termed handedness.

High-level tasks comprise novel, fine-tuned motor acts that are demanding both spatio-temporally and in terms of complex cognition. At the population level, subjects are expected to be asymmetrically distributed, as a reflection of underlying cerebral hemispheric specialization, so that the majority in any given group are biased to one side or the other. Examples of high-level tasks are superimposed task demands such as unnatural postures or precise object manipulation. This, they termed manual specialization.

Although Fagot and Vauclair (1991) are careful to point out that their dichotomy is really a graded continuum, they do not provide gradations. This is problematic because each category is a multifactorial composite, that is, several variables are confounded. What is one to do with a routine but complex act like nutcracking in chimpanzees? Or a novel but simple act like reaching

for food suspended overhead? How many trials are needed before newly experimentally induced bipedalism becomes familiar? What to do about the same subjects tested repeatedly, but each time on a new variant of a task? Testing Fagot and Vaucclair's (1991) model requires being able to distinguish such tasks as high or low level.

Theoretical perspectives referred to so far are all of one type of asymmetry proposed by van Valen (1962): Anti-symmetry, in which competitive interaction between left and right sides results in bilateral differences. Another type, fluctuating asymmetry, could in principle be involved in hand laterality, though so far as we know, it has never been invoked. Fluctuating asymmetry consists of small deviations that arise from environmental or genomic stress, and the individual's ability to survive such deviations provides a direct indicator of phenotypic quality. Traits under the influence of sexual selection are especially strongly affected, in a variety of animal species, including humans (e.g. Swaddle and Cuthill, 1994; Gangestad et al., 1994), but the only applications of fluctuating asymmetry theory to nonhuman primates that we know of is to structure, not behavior (Manning and Chamberlain, 1993, 1994).

Other piecemeal attempts at a theory of laterality for primates exist—Reynolds's (1991) "triped theory" that considers the dominant hand to be an unpaired organ—but no single theory tackles even the most basic evolutionary question of all, which is why any organism should ever depart from random symmetry or why any set of organisms should do so in concert. Meanwhile, there is a multitude of humble, practical issues to be faced up to dealing with laterality of hand function (Ward, 1997a).

STATISTICAL ISSUES

For an individual with sagittally paired organs, the null hypothesis is the simplest possible: Use one or the other at random. That is, in probability terms, $p = q = .50$. Thus, a real departure from randomness is a statistically significant deviation from 50:50 for left vs. right. Such a bias is usually termed asymmetrical for structures, such as cerebral hemispheres, or lateral for func-

tions, whether physiological or behavioral, such as hand use. (This applies whether one hand is used singly, or two hands are used jointly, in obligatory complementary roles. Clearly, it does not apply when two hands are "yoked" in simultaneous, identical roles, as in doing push-ups.)

There is a third option, however, when dealing with populations of individuals, who may be classified as 1) left-biased, 2) right-biased, or 3) unbiased. What then should be the null hypothesis? A few laterality studies (e.g. Deuel and Schaffer, 1987; Parr et al., 1997) have assigned each category a probability of .33, but none has presented a rationale for what seems to be an arbitrary scheme. One line of argument might be to assume that hand use is normally distributed and that any subject who is biased to left or right beyond one standard deviation from the mean of 50 L:50 R is truly lateralized. This line of reasoning would yield a null hypothesis of 16 L:68 Unbiased:16 R.

Most studies that focus on laterality of function ignore this issue, however, preferring to test the ratio of left-sided to right-sided individuals remaining after having set aside ambilateral individuals. This can be misleading when most members of a population are unlateralized, yet play no part in analyses e.g. Fagot and Vaucclair (1991, Table 1).

Whether or not the data are drawn from a normally distributed population is one of several criteria (usually assumptions) that determine whether laterality researchers use parametric or nonparametric statistical tests (Siegel and Castellan, 1988). Typically, behavioral data seldom meet these strict criteria, and so in general the less stringent nonparametric tests should be preferred on the general principle of conservatism. In practice, published reports on laterality rarely refer to such issues, although there are admirable exceptions (e.g. Ward, 1995). Instead, some studies consistently use parametric tests, or nonparametric tests, or alternate between them, or occasionally use both on the same set of data. Given that many laterality data are nominal (that is, a data-point constitutes an individual who is classified as Left, Right, or Ambilateral), then the statistical test must be nonparametric, e.g.

Binomial test. In general, it seems best to stick to nonparametric statistical tests, unless the case is explicitly made to justify parametric ones.

In behavioral research in general, two-tailed regions of rejection are preferred to one-tailed, on grounds of conservatism. In laterality research, this means that an hypothesis should be framed in terms of a difference from randomness, rather than in terms of the direction of difference, unless there are compelling, independent reasons for predicting directionality. For example, in a study in which the independent variable was cerebral asymmetry, one might justifiably predict bias in the hand function of the contralateral limb. The same reasoning works in reverse: When laterality of function is the independent variable, then one can reasonably predict corresponding asymmetry of structure. What is not acceptable in most studies of nonhuman primates is to use the human primate's species-typical condition to predict right-handedness in other species, given that *Homo sapiens* is so aberrant. Most studies of laterality of hand function use two-tailed probabilities, but some do not.

In choosing a level of significance (α), most researchers in laterality studies select .05 in seeking to avoid Type 1 errors, that is, rejecting the null hypothesis of randomness when it is true (cf. Ward, 1995). (Only a few studies fail to specify the level of significance used.) More recently, some studies have adopted the more strict level of .01 (Milliken et al., 1989; Mason et al., 1995; Mittra et al., 1997). One reason for the latter is when many statistical tests are performed, for example, if 10 subjects are tested on 10 variables, yielding a total of 100 tests, then at $\alpha = .05$, on average, five results will be spurious, that is, Type 1 errors indicating laterality. This hazard of false-positive results is seldom made explicit, but it is always a potential problem (Siegel and Castellan, 1988).

The single-most vexing issue in laterality research may be that of the independence of data-points (Martin and Bateson, 1993). That is, the occurrence of an event must not bias the chances of the occurrence of another equivalent event, if each is to be counted as a

separate data-point. Suppose we were interested in the hand preferences of card dealers in a casino. We might record each card placement as a deck is dealt out, giving us 52 ostensible data-points. Having watched five dealers each make one such deal, what can we conclude statistically about card dealing, the casino, or each dealer? Nothing. For card dealing in general, casinos are specialized contexts with particular rules, so to draw any valid conclusions means collecting data from a wider range of contexts. This will help avoid within-group or "litter" effects (Martin and Bateson, 1993). For the casino, the apparent N (sample size) of 260 (5×52) events is actually an N of only five deals, and even if all the card placements in all of the deals were made by right or left hands, these are not enough data to detect laterality (when $N = 5$, $x = 0$ exceptions, $P = .06$, two-tailed Binomial test). This invalid use of multiple measurements from single individuals (i.e. 52 card placements from each dealer) is called the "pooling fallacy" (Machlis et al., 1985).

Finally, for similar reasons, we can say nothing with these data about the laterality of the individual dealer, for instead of $N = 52$, it is only $N = 1$. (Of course, if in the middle of a deal, say after placing 18 cards, the dealer puts down the deck of remaining cards, then scratches her nose, then picks up the remaining 34 cards and completes the deal, we might then have $N = 2$ data-points, depending on what constitutes a satisfactory criterion of independence of consecutive events. This is not, strictly speaking, a statistical issue but is instead one of measurement, to be dealt with in the next section.) In laterality research, the analogous situation is often some variant on a single-caged monkey repeating trial after trial of reaching through the front of a cage to retrieve small food-items, in blocks of 20–100 trials.

The general point is that the power of a statistical test increases with an increase in sample size (N) (Siegel and Castellan, 1988). Consider a subject who did 67% of responses with her left hand: For $N = 3$, 2 Lefts vs. 1 Right are too few data, even if the individual does perform twice as many acts with her left hand. Even for $N = 30$, with 20 Lefts vs.

10 Rights, $z = 1.64$, for which $P = .10$, two-tailed, a no-difference result. But for $N = 300$, so that 200 Lefts vs. 100 Rights, $z = 5.72$, the chances of the left bias not being real are $P = .00001$. Clearly, laterality researchers must take great pains to avoid inflated sample sizes, but unfortunately this is not always the case.

In summary, the ideal statistical treatment of laterality data involves using non-parametric tests, both within and across subjects, that are two-tailed at a level of at least $P = .05$, set against a realistic null hypothesis. Special attention must be paid to sample size, avoiding invalidating inflation. Finally, all of the above details should be presented in the published report, along with the raw data (R's and L's) on a subject-by-subject basis.

MEASUREMENT ISSUES

The most essential point in laterality research is when to consider an individual or population to be lateralized, yet there is a surprising lack of consensus in criteria. For some researchers, a simple majority of responses to one side by an individual (Hopkins et al., 1993b) or of members of a population thus lateralized is enough (Lehman, 1970). So, if 51% of the individuals in a sample show 51% of their responses to one side, laterality of hand function is proven at both levels. A more stringent criterion is to set an arbitrary percentage threshold for either or both problems, sometimes taking into account a minimum number of responses or individuals: >60%, King, 1995; >70%, Deuel and Dunlop, 1980; > 80%, Warren, 1953; >90% Gautrin and Ettlinger, 1970. The only secure designation is to consider an individual or population lateralized only if it departs significantly from 50:50, based on appropriate statistical testing.

Alternative views abound: If all 10 individuals show 51% of their hand use to the left, then that population is weakly but truly lateralized (Binomial test, $N = 10$, $P = .002$, two-tailed), even if no individual is lateralized. Further, since population-level lateralization is an abstraction, based on some arbitrary set of proportions, it may be argued that it takes only one lateralized indi-

vidual in a population for that population to be lateralized (Ward, 1991).

When an individual uses one hand repeatedly to perform the same task, e.g. picking up item after item from the floor, how is one to decide if consecutive responses are independent of each other? In other words, how to distinguish events from bouts of events? (In the example given above, one uninterrupted deal was one bout of 52 nonindependent events.) Three sorts of criteria are usually used in laterality research: Temporal, manipulative, or behavioral. The greater the interval between successive events, the more likely these are to be independent: Consider the difference between a pause of a second, a minute, an hour, or a day. Such temporal demarcations, usually in seconds, are used in laterality research, but we know of no empirical attempts to justify the intervals chosen. E.g. for Vauclair and Fagot's (1987a) study of baboons, a pause of more than 1 second was enough to count an act (= data-point) as occurring again.

Manipulative criteria are those in which experimenters facilitate or enforce changes in the context that break up the stream of the subject's behavior. For example, placing the objects to be picked up in different locations forces the individual to reach to different spots (Sanford and Ward, 1986). Requiring the subject to move to the other side of the test-cage between trials helps to preclude stereotyped use of a manipulum by a sedentary subject (Lehman, 1978). Distributing in space the objects to be handled by the subjects so that they have to change postures or locations between responses is another effective technique (Olson et al., 1990).

Many of these temporal and procedural safeguards have long been used in experimental psychological studies of laboratory primates, where perseveration effects and position habits were recognized as inadvertent by-products of research protocols (Lehman, 1991). However, with the rise of more observational or ethological methods of data collection, in which subjects and settings are less controlled, such problems of sequential stereotyped responding may also emerge (Fagot and Vauclair, 1991).

The clearest safeguard in establishing independence of behavioral data-points is when a different behavioral pattern performed by the same hand intervenes between two instances of the same pattern. For example, if a monkey plucks a fruit, then scratches herself, then plucks another fruit, all with the same hand, we have good reason to count the two plucks as independent events (McGrew and Marchant, 1992; Panger, 1997). (Of course, consistently interviewing behavioral patterns can themselves be sources of complicating bias!) Another way of insuring the same result is to count only the first response in a string of the same pattern, until the subject of study either changes hands or changes patterns (Boesch, 1991; Westergaard and Suomi, 1996a). A safe and straightforward solution is to take only one datum per day per subject (Hopkins, 1994).

To reiterate the danger of inflated N's, consider the following hypothetical example: An ape performs 56% of his self-scratches with his right hand and 44% with his left. Is he lateralized? With $N = 50$ instances, that is, 28 R vs. 22 L, he is clearly unlateralized, since $z = 0.71$, $P = .24$. However, if $N = 500$, that is, 280 R vs. 220 L, then the difference is highly statistically significant: $z = 2.64$, $P = .008$.

Except for Ward's (1995) group studying prosimians, few studies of laterality report formal reliability testing of single (intra-) or multiple (inter-) scorers or observers (cf. Hopkins, 1994). Presumably this is because of the simple discrimination (left vs. right) and the basic behavior of hand use recorded: Most studies report some variation of an individual's reaching to pick up and retrieve a small object. However, even this is not easy: MacNeilage et al. (1987) proposed a descriptive classification of six different kinds of reaches: Simple, complex, expose-and-reach, stabilize-and-reach, retrieve-and-reach, manipulate-and-reach.

Issues of validity (that is, the extent to which a variable actually reflects the phenomenon it purports to measure) are another matter, however. The single most common task used in laterality research, picking up a small item from a smooth, horizontal surface, rarely occurs in nature. Presum-

ably, primate hands were not subject to natural selection for such tasks, and any proficiency at them is more reflective of human protocols than of evolved abilities: "Picking things up from a flat surface is far more difficult for a primate than grabbing what swings in mid-air" (Bishop, 1964, p. 222). Instead, primate foraging usually involves extracting, processing, or pursuing food, whether plucking a berry, stripping a pith, or snatching at an insect. Natural tasks are rarely feasible in captivity but can be ingeniously simulated: King and Landau (1993) had squirrel monkeys capture freely swimming goldfish from containers as big as tubs; Butler et al. (1995) tied sheaves of bamboo stalks to upright structures in an enclosure, then recorded the species-typical food processing of gentle lemurs.

Ethologists have long stressed the value of recording spontaneously exhibited, specifically and explicitly defined, and descriptively labeled behavioral categories, preferably in exhaustive and inclusive repertoires, or ethograms (Martin and Bateson, 1993). This is tedious and time-consuming but has been done in studies of hand use in primates (Marchant and McGrew, 1996). Sometimes, even greater precision is needed: Byrne and Byrne (1991, 1993) broke down four patterns of plant food processing done by mountain gorillas, showing that only at the level of component subunits was laterality crucially expressed.

Questions of ecological validity also emerge when captive primates are induced to perform acts that they rarely or never show in nature. For example, bipedal stance (see below) enhances chimpanzee laterality of hand use in cages (Hopkins, 1993), yet wild chimpanzees rarely go bipedal in nature (Doran, 1993; Hunt, 1992). The baseline condition for studies of gibbons and orangutans is on the ground or floor, that is, terrestrial (Olson et al., 1990), but in nature these Asian apes are almost exclusively arboreal (MacKinnon, 1974; Hunt, 1996).

Gross, composite categories of hand use are convenient to record but may yield confusion: Dimond and Harries (1984) recorded a general category called "face touch" that ranged from scratching to burying the face in the hands. They claimed to have found

species differences in this easily recorded but functionally confounded category, but Suarez and Gallup (1986) failed to replicate their results. Aruguete et al. (1992) recorded face touching (but excluded scratching) in squirrel monkeys and chimpanzees, but found no laterality in either species. Rogers and Kaplan (1996), studying released Bornean orangutans, broke down face touching into three subcategories, only two of which were lateralized. It seems likely that these conflicting results may stem from recording different behavioral patterns under a general rubric, e.g. self-grooming may well differ functionally from displacement scratching or from slapping at insects, yet all could result in the face being touched.

METHODOLOGICAL ISSUES

Species

Early studies of hand laterality sometimes failed to specify the type of primate involved (Franz, 1913; Warren, 1958; Ettlinger et al., 1968), but modern studies almost always work on the level of species (cf. Yuanye et al., 1988). Few studies specify subspecies (Gijzen, 1972; Rogers and Kaplan, 1996; Stafford et al., 1993), but little research on laterality has tested subspecies as a discriminative independent variable (cf. Groves and Humphrey, 1973). Occasionally, researchers work at the level of genus, lumping two or more congeneric species: *Hylabates* (Stafford et al., 1990), *Lemur* (Masataka, 1989; Ward et al., 1990), *Cebus* (Masataka, 1990), *Macaca* (Hatta and Koike, 1991). Few studies have focused on closely related species as the sole independent variable while holding all others constant, but Lehman (1978, 1980) found no difference between *Macaca mulatta* and *M. irus* in reaching to pick up fruit.

More worrying is when taxon is confounded with other variables, especially major ones such as captive vs. wild (see below). Almost all studies of captive capuchin monkey laterality have been done on *Cebus apella* (Anderson et al., 1996; Frigaszy and Mitchell, 1990; Limongelli et al., 1994; Parr et al., 1997; Westergaard and Suomi, 1993a), while the only field work on the genus so far has been on *C. capucinus* (Panger, 1997). Similarly at the level of subspecies, apart

from one early study (Gijzen, 1972), all captive laterality research on gorillas has been done on the western lowland gorilla, *Gorilla g. gorilla* (Annett and Annett, 1991; Fagot and Vauclair, 1988a; Heestand, 1986; Manning and Chamberlain, 1990; Olson et al., 1990; Shafer, 1993), while the only hand laterality research done in nature has been on mountain gorillas, *G.g. beringei* (Byrne and Byrne, 1991, 1993).

Certain taxa of primates have been neglected in hand laterality research. Among the prosimians, we know of no studies on indri (Indriidae), lepilemurs (Lepilemuridae), or tarsiers (Tarsiidae), presumably because of low numbers in captivity and difficulty of access in nature. Among New World monkeys, we know of no studies of owl monkeys (Aotinae), or sakis (Pitheciinae), and only one of ateline monkeys (Laska, 1996b, on spider monkeys, *Ateles geoffroyi*). Of the Cercopitheciinae, Old World monkeys, we know of no published results on any of the following genera: *Allenopithecus*, *Mandrillus*, or *Miopithecus*. Of the eight genera of colobine monkeys, only two, *Presbytis* and *Rhinopithecus*, seem to have been studied (Yuanye et al., 1988; Mittra et al., 1997).

In summary, investigators of laterality in primates should be as precise as possible, preferably to subspecies, in identifying their subjects, and efforts to fill the taxonomic gaps should be undertaken.

Age

Early studies of behavioral laterality, mostly on macaques, focused on immature subjects, at least as can be inferred from low body-weights (Lehman, 1970; Warren, 1977). This raises the problem of false-negative (Type-2 error) results, if immature neuromuscular development means not-yet-lateralized performance (MacNeilage et al., 1987). Most studies of the ontogeny of laterality of behavior in primates show increased lateralization with age, at least up to adulthood, although most such studies are cross-sectional (Ward et al., 1990; Stafford et al., 1990; Hopkins and Leavens, 1997) rather than longitudinal (Bard et al., 1990; Hopkins, 1995b; Hopkins and Bard, 1993a). However, other studies suggest the opposite: Immatures may be more rigid (one-sided) in

their hand use while adults may be more flexible (McGrew and Marchant, 1992; Boesch, 1991). Finally, some studies have found no correlation between hand laterality and age, however large the sample ($N = 116$ female Japanese macaques, Takeda, 1994; $N = 18$ Guinea baboons, Vauclair and Fagot, 1987a; $N = 67$ rhesus macaques, Brooker et al., 1981). We know of no studies of the stability or deterioration of laterality with senescence.

More recent studies tend to limit their data to adult subjects, on the grounds of homogenous, completed maturation (Mittra et al., 1997), or attempt to cover the entire lifespan, by observing infants as soon as they achieve motor independence through to old age (Takeda, 1994; Marchant and McGrew, 1996; Hopkins and Leavens, 1997).

The ideal study has sufficient numbers of subjects throughout the age range to enable statistically valid comparisons across age classes. Even better would be longitudinal studies from birth that would enable ontogenetic progress, such as the effects of caretakers' laterality, to be tracked from the outset.

Sex

Sex (or gender) as the major independent variable has played little part in studies of laterality of function, perhaps because except for genitals, the two sexes share the same set of paired organs. Therefore, a priori, there is no reason to expect sex differences, when arguing from structure to function. There may be nonhuman primate counterparts in brain structure to the sex differences reported for *Homo sapiens*, and some researchers of nonhuman primate laterality have sought to explain their findings in terms of human sex differences in brain and behavior, e.g. Milliken et al. (1989), Ward et al. (1990).

Most studies with large numbers of subjects matched on other variables have failed to find sex differences in bimanual hand laterality (Byrne and Byrne, 1993, $N = 28$ mountain gorillas; Colell et al., 1995b, $N = 24$ chimpanzees; Hopkins, 1994, $N = 140$ chimpanzees).

Fewer studies have found sex differences: Shafer (1993) for 43 captive gorillas, found more males than females to be lateralized

overall to the right. For 19 captive gibbons, Stafford et al. (1990) found females to be more lateralized and to show a greater propensity for right hand use as they aged than males. Hopkins and Leavens (1997) reported similar results for 115 captive chimpanzees. For 194 lemurs of 6 species, males of all age groups showed a clear left-hand bias, but females did not (Ward et al., 1990).

A conspicuous functional difference between the sexes concerns mammary glands. Since only females lactate, any hand use related to suckling might emerge as a sex difference in laterality. The most extensive ($N = 52$) study showed the cradling of chimpanzees and gorillas to be lateralized to the left, and of orangutans and gibbons to be unlateralized (Manning et al., 1994). However, their measure was not of the mother's differential hand use, but of the position of the infant's head on the left or right side of the mother's chest. More intensive studies with multiple measures, including maternal holding of the infant, have found no laterality in mother-infant pairs of chimpanzees (Hopkins et al., 1993a; Dienske et al., 1995). Rhesus monkey mothers show no difference between the hands in cradling or retrieval, but use their left hands more often to carry their infants (Tomaszycki et al., 1997). We have found no other evidence of lateralized cradling in other species of primates, but Hatta and Koike (1991) found that seven of eight macaque (*Macaca* spp.) mothers used their left hands to retrieve their infants in response to an alarming stimulus.

Sex is an easy variable to record, and given that sex differences in hand use in *Homo sapiens* are well-known, it bears attention, even in the absence of theoretical expectations.

Setting

Behavioral laterality of hand function was first studied in the laboratory (Franz, 1913; Kounin, 1938; Finch, 1941) and only later in the wild, usually as a by-product of an overall field study (Schaller, 1963; Nishida, 1973). However, the purported artificial vs. natural dichotomy is actually a continuum: from solitary laboratory cage, to group-housed enclosure in a zoo, to naturalistic island in a safari park, to released or rehabili-

tated co-existence, to natural habitat. Clearly, a multitude of variables accounts for the differences between these settings; a few that co-vary with the above continuum and that might specifically affect laterality of function (but likely not symmetry of structure) are: amount of space and external stimuli available, interaction with humans, extent of asymmetrical environment. To elaborate: subjects that cannot climb are unlikely to develop a stronger limb for tripedal positional support; subjects deprived of large objects are unlikely to develop complementary bimanual handling skills; subjects raised by right-handed human caretakers are likely to acquire right-handed biases; subjects living in asymmetrical cages are likely to show corresponding laterality. We know of no empirical studies of such potential effects in primates, although these are known in other species (Collins, 1975).

Instead, careful experimenters have sought to control for such potential effects whenever possible: by presenting stimuli in the subject's midline (Hopkins and Bennett, 1994), by alternating hands when offering stimuli to subjects (Lehman, 1968), by recording data from the same subjects in different settings (Marchant, 1983; Fagot and Vauclair, 1988b; Vauclair and Fagot, 1987a).

No study has compared the behavioral laterality of the same individuals in captivity vs. in the wild, although in principle this could be done with prerelease vs. postrelease data in rehabilitation projects (Rogers and Kaplan, 1993, 1996). Instead, Shafer (1987) showed that most of 27 captive-born gorillas were lateralized for hand use while their 20 wild-born counterparts were not. Hopkins (1994) found that 60 mother-reared chimpanzees were more lateralized than were 80 chimpanzees reared by humans in a nursery from their first month.

In general, the more natural the setting, the more valid the results are likely to be, on the principle that an organism's performance will be more representative with closer approximation to the environment of evolutionary adaptedness. If nature is essentially symmetrical, at least to a mobile organism, then powerful forces of natural selection would be needed to produce laterality.

Sensory modality

Most studies of hand use in primates focus on the visual modality, that is, eye-hand coordination leads to visually guided movement, at least when there is a target object. So predominant is the sense of vision that its function usually is assumed, but in principle, hand use could be prompted or guided by any modality: sound, smell, or touch. (However, only with the haptic sense does the hand act both as a sensory organ of touch as well as a motor organ.) In practice, only the tactile or haptic modality has been investigated: Hoerster and Ettlinger (1985), summarizing a battery of research on rhesus monkeys in the laboratory, found that 77 left-biased individuals reached a tactile criterion faster than did 78 right-biased counterparts. Fagot et al. (1991) compared rhesus monkeys on five tasks of visual or haptic stimuli, e.g. extracting unseen peanuts from a matrix of pebbles, and found a stronger bias in the tactile tasks. Parr et al. (1997) studied 22 capuchin monkeys in similar tasks of extractive foraging, and also took account of posture. All studies found greater left-sided lateralization in tactual as compared with visual tasks.

We know of no studies in which other sensory modalities influenced hand use, although there are many direct studies of lateralized function of bilateral paired sensory organs (e.g. Hauser and Andersson, 1994).

Sample size

The single most vexing methodological issue is also the simplest one: how many subjects or measures or instances should be studied? More is surely better, but how much is enough? On statistical grounds, a minimum of six cases are needed to produce a statistically significant result (Binomial test, $P < .05$, two-tailed). Thus, if six of six subjects are biased to one side, we can consider that population lateralized (or eight of eight at $P < .01$). Larger samples are needed if the sample is to be subdivided, for example into males and females: if all four males are more lateralized than all four females, then a sex difference exists (Mann-Whitney U test, $U = 0$, $P = .028$, two-tailed).

Since laterality effects are rarely all-or-nothing, larger samples are usually needed.

For subjects, the range of numbers per published study is from one, usually case studies of exceptional individuals (Cunningham et al., 1989), to 140 chimpanzees (Hopkins, 1994) to 277 rhesus monkeys (Hauser et al., 1991). Sometimes, numbers of subjects are limited by availability: Mason et al. (1995) studied all 15 sifakas (*Propithecus verreauxi coquereli*) in captivity outside of Madagascar. For the rare aye-aye, *Daubentonia madagascariensis*, parallel studies on both sides of the Atlantic yielded a total of only 11 subjects available in captivity (Feistner et al., 1994; Milliken, 1995). In a meta-analysis of 78 published studies of laterality in apes, the modal number of subjects was one, and the median was 3.5 (Marchant and McGrew, 1991), but recent studies have tended to be more ambitious.

For measures (or tasks or variables), Marchant and McGrew (1991) found that the modal number of measures was one, and the median was three, in 68 studies of apes. In the most extensive studies done in laboratories, Welles (1976) used 31 measures of prehension for seven species of primates, and Beck and Barton (1972) used 17 tasks of manipulation for 10 stump-tailed macaques, *Macaca speciosa*. In the wild, Marchant and McGrew (1996) recorded 43 categories in an ethological study of the chimpanzees of Gombe, and 50 categories for the same species at Mahale (unpublished data), but many of these behavioral patterns occurred too rarely for comprehensive statistical analyses.

For trials (or events), there is much variation, particularly in observational studies of spontaneous behavior, as opposed to scheduled blocks of trials in laboratory experiments. In 44 studies of apes for which data were available, the "average" number of trials per subject per task was 113, but the range was from 10 to 900 (Marchant and McGrew, 1991). The most prolific study by far was Shafer's (1987), who recorded 53,750 acts in 10 categories from 47 gorillas in five zoos! Eating accounted for 20,156 instances, as the most frequent category, but the resulting data-points are unlikely to be independent.

For sample size, whether of subjects, measures, or trials, more is better, especially in complex, multivariate analyses. Much of the (earlier) published literature is bedeviled by confusing, small-sample-size effects.

SPECIAL TOPICS

Preference vs. performance

Laterality of function may be manifest in terms of preference (frequency) or performance (proficiency), with the former being far more often investigated. The former yields a variety of derived measures, apart from the basic ratio of Left:Right. For example, Hopkins (1994) used a handedness index (HI) in order to map all degrees of bias on a single scale from 0 (100% left) to 1 (100% right) and an absolute handedness index (ABS-HI) that represents overall strength of bias from 0 (no bias) to 1 (100% bias). Other authors have used variations on the same indicators (Fagot et al., 1991), but all are variants on how many times the two hands are used.

Measures of performance take three main forms: rate of success, rate of failure, or productivity. We might expect natural selection to have favored more lateralized individuals if they had greater numbers of successful responses per unit time, fewer errors per unit time, or higher payoffs per response. In terms of individual hand use, we would expect the preferred hand to be more successful and productive and to make fewer errors.

In experimental settings: Frigaszy and Mitchell (1990) for capuchin monkeys showed that the preferred hand was quicker in a box-opening task, when level of difficulty was taken into account. Right-preferent rhesus monkeys were faster to reach criterion and showed shorter latencies in using a joystick than were their left-preferent colleagues (Hopkins et al., 1992). Rigamonti et al. (1997) showed in pigtailed macaques both types of effects in a simulated foraging task of removing embedded food pellets: the preferred hand made fewer errors, whether it was the left or right; the left hand was quicker than the right, whether it was preferred or not. Cottontop tamarins reaching to get food-items from a moving turntable were more accurate with their

preferred hand, and the more lateralized individuals made fewer errors (King, 1995). For apes, Marchant and Steklis (1986) found that chimpanzees' left and right hands differed on bar pressing rates, but this was not correlated with other measures of handedness.

In observational studies: Butler et al. (1995) found that for gentle lemurs (*Haplorhina griseus*), bamboo processing patterns in foraging were done more quickly with the preferred pattern, on an individual basis. Squirrel monkeys reaching to capture live goldfish from a pool showed a negative correlation between strength of hand preference and error rate: the more lateralized individuals got more fish (King, 1995).

The only systematic study of performance done in nature showed that wild chimpanzees exclusively committed to one hand in using tools to fish for termites were more efficient than were individuals who used either hand (McGrew and Marchant, 1997a): They got more termites per withdrawal of the probe, on average.

Posture

Of necessity, laterality of hand function is related to posture, because, with rare exceptions, a limb providing postural support is not available to do anything else. Obligate quadrupeds such as ungulates must manipulate food with their mouths, as no limbs are free to do otherwise. A biped, whose weight is supported solely by its two hindlimbs, has a true choice of using either forelimb to perform a one-handed task. When postural support must be at least tripodal, as in most arboreal positions, then the organism must choose which forelimb, left or right, to deploy for support vs. other functions. Clearly, bimanual hand use is only possible in an upright posture, when both hands are free of supporting roles. This is presumably why most object manipulation by primates is done while sitting, which is the overwhelmingly predominant posture for hominoid primates (Hunt, 1996). All of this is merely the basic ecology of biomechanics, but it is rarely made explicit in studies of laterality.

Homo sapiens is an anomaly among primates with its habitual, unassisted, upright, bipedal posture both in stance and

locomotion. Other primates typically stand bipedal only occasionally, either by squatting or by rising upright with assistance from one or both forelimbs. This manifests another variant of tripedalism or quadrupedalism, the issue being not what proportion of the body-weight rests on which limbs, but rather which limbs are committed to support and so are unavailable for other activities. Humans are the only primates for whom bipedal locomotion is the norm, and some primates, e.g. gibbon, sifaka, indri, travel bipedally on the ground only abnormally, when unnaturally forced to descend from their arboreal environment of evolutionary adaptedness. Orangutans being rehabilitated back into the wild by humans readily travel bipedally, but their wild counterparts are not seen to do so (MacKinnon, 1974, p. 38).

Posture was rarely mentioned in hand laterality research until after MacNeilage et al.'s (1987) article appeared, presumably because experimental studies typically tested sedentary subjects seated or standing terrestrially. Since then, more and more studies have incorporated posture as an independent variable, either by recording its spontaneous performance (Diamond and McGrew, 1994) or by inducing it (Anderson et al., 1996; Olson et al., 1990; Roney and King, 1993). Some studies have facilitated the repertoire of natural postures (e.g. vertical climbing) by manipulating settings or stimuli (King, 1995), while others have elicited unnatural posture by repeatedly rewarding subjects for standing bipedally to get food (Hopkins, 1993; de Vleeschouwer et al., 1995).

Bipedal posture (usually assisted, e.g. by clinging to the mesh of a cage front) has been found to enhance lateralization of hand use, as compared with the same individuals' responses while sitting (usually squatting) or standing tripodally or quadrupedally on the floor (Hopkins, 1993; Larson et al., 1989). Other studies have found no differences in laterality of hand function across postures, either across all recorded behavior (Dodson et al., 1992) or across some measures but not others (Diamond and McGrew, 1994). One study found a reverse effect: rhesus monkeys were significantly lateralized to the left

when standing quadrupedally but were not biased when standing bipedally (Westergaard et al., 1997a).

Rarely, however, do studies simultaneously record what the "other" hand was doing while the operative hand performs a one-handed task. Was the other hand available as an option, or was it committed to some other function, such as postural support? Aruguete et al. (1992) studying 27 captive chimpanzees recorded data on hand laterality only when both hands were "free," that is, available to be used. Marchant and McGrew (1996) found for wild chimpanzees that one hand was idle in only 10% of bouts of manual activity; in all other cases, both hands were active or the other hand provided support.

The most common postures in the activity repertoires of primates are those of resting (sit, recline, lie) in which the torso and not the limbs absorb most of the body's weight, leaving some or all of the limbs free (Hunt, 1996). We know of no study of laterality of hand function that has looked at such postures even minimally, much less exhaustively.

In the ideal study of hand laterality in primates, posture is recorded as an independent variable, and all forms of postures shown are clearly defined, including other points of support for the body. (An ateline monkey can hang suspended from only its prehensile tail, leaving all four limbs available for other uses!) When other than quadrupedal posture is exhibited, then the use of all limbs, not just the one doing a task, should be noted.

Bimanuality

Most studies of laterality of hand function focus on one-handed tasks and ignore what the other hand is (or is not) doing. When two-handed tasks occur, these take four forms: 1) both hands operate simultaneously and identically on the same object, e.g. a chimpanzee double-slaps the ground with open palms; 2) both hands operate alternately, but identically, e.g. a gorilla beats its chest; 3) both hands operate simultaneously but complementarily on the same object, e.g. one hand holds a fruit while the other hand gouges out its contents; 4) both hands operate simultaneously but do different tasks,

e.g. one hand holds a fruit while the other hand self-grooms.

For the first type, no laterality is possible, as by definition the act is symmetrical, or yoked. (Vauclair and Fagot, 1987a, called these bilateral bimanual activities.) The second type occurs rarely in primates, e.g. drumming in chimpanzees, although Schaller (1963) found that the right hand was used to start sequences of chest-beating in mountain gorillas. The big exception, however, is locomotory gaits, i.e. when limbs are repeatedly moved in sequence. Some studies have looked at the "leading limb," i.e. the one that leads off a bout of locomotion, but this often is unspecified as either arm or leg (Heestand, 1986; Hopkins et al., 1993c) or is specified as the leading leg (Marchant and McGrew, 1996). There are few studies in primates of the leading hand used to grasp the substrate in initiating climbing, brachiation, etc. (Heestand, 1986; Stafford et al., 1990).

The third type has received the most attention. Hopkins (1995a) called it coordinated bimanual activity because the two hands work together to accomplish one goal (but this definition would also apply to types 1 and 2). In a monumental study of 110 captive chimpanzees, Hopkins (1995a) reported population-level laterality when the apes used their index fingers to extract peanut butter from a plastic tube held in the other hand. In such cases, the hand performing the more gross, less skilled component, often with some form of power grip, is termed the subordinate hand, while the dominant hand is the one doing the finer, more skillful component, often with a precision grip. In nature, this type rarely occurs in eating but occurs most often in grooming (Marchant and McGrew, 1996).

The fourth type has rarely been systematically studied. Marchant and McGrew (1996) found that most bouts of eating by wild chimpanzees consisted of the diner consuming one food item held in the dominant hand while the subordinate hand held other, yet-to-be eaten foodstuffs. For the same behavioral pattern in 140 captive chimpanzees, Hopkins (1994) showed a right-side bias for eating and a left-side bias for holding, with adults more lateralized than subadults.

It should be clear that bimanuality in studies of laterality of function requires explicit and precise operational definition of the roles of each hand: Sometimes the same task can be solved either unimanually or bimanually (Fagot and Vauclair, 1988a, lowland gorillas; Fagot and Vauclair, 1988b, Guinea baboons; Hopkins and Rabinowitz, 1997). Given that some primates are quadrumanous, the same care should be taken when hand and foot, or the two feet, act in concert.

Inheritance

In *Homo sapiens*, handedness is genetically influenced, as shown by twin and cross-fostering studies (McManus, 1991). Only one such study has been done with nonhuman primates (Hopkins, 1997); instead investigators have sought to see if laterality of hand function follows family lines. Success has been limited: failure to find concordance in hand laterality between parents and offspring may sometimes have foundered because only maternal and not paternal kinship was known (Brooker et al., 1981; Vauclair and Fagot, 1987a; Takeda, 1994). Hopkins (1997) compared full and half siblings (both maternal and paternal) raised by their mothers and by human surrogates in chimpanzees. He found strong concordance for maternal but not paternal effects, regardless of rearing condition.

The most exhaustive study of the heritability of hand preference was by Hopkins et al. (1993a) of 76 captive chimpanzees: they found both paternal and maternal effects on offspring's hand bias, and half-siblings also more closely resembled one another than expected by chance. This contrasts with Byrne and Byrne's (1991) study of wild mountain gorillas, in which mother-offspring, father-offspring, and full-sibling pairs showed no significant effects, and with Westergaard and Suomi's (1997) study of captive tufted capuchin monkeys, in which neither mother-offspring nor father-offspring effects occurred in extracting a grape from a tube.

The origins and determinants of laterality could most easily be done by comparing the correlations between same-sex dizygotic vs. monozygotic twins in the Callitrichidae, assuming all other things being equal. Matoba

et al. (1991) found for common marmosets that laterality in reaching for food by offspring was significantly correlated with mothers' but not with fathers' laterality. Since both parents share in the caretaking of offspring, the obvious candidate explanation that maternal nurturing influence should be predominate, seems insufficient (cf. Hopkins, 1997).

With the availability of DNA typing to elucidate genetic kinship, more studies of the nature and nurture of laterality of function may be able to resolve such conflicts in results.

Arm asymmetry

The simplest explanation for laterality of hand function may be upper limb asymmetry of structure, as found in *Homo sapiens* (MacNeilage et al., 1987). Putting aside the vexing problem of chicken-and-egg, there is little published evidence comparing the mass or dimensions of muscles and bones in the left and right arms of nonhuman primates. Dhall and Singh (1977) claimed to find right limb dominance in the weights of forelimb muscle and bones in 12 rhesus macaques, but none of the results holds up to statistical scrutiny. However, Falk et al. (1988) found significant right-biased differences in some dimensions of the humerus and ulna in 150 rhesus monkeys. Helmkamp and Falk (1990) found few left-right differences in the forelimb bones of 137 rhesus monkeys, but all of them favored the right side. In none of these studies was the functional laterality of the subjects known.

Morbeck et al. (1994) compared dimensions, weights, and mineralization across arm bones in 11 wild chimpanzees; most of the 51 comparisons yielded no difference, but of the five statistically significant differences found, all favored the right side. Six of the individuals were lateralized for termite fishing (McGrew and Marchant, 1992), but there was no relation between the limb preferred for this task and upper limb asymmetry. This is not surprising, given that termite fishing is a seasonal, low-impact activity, reliant more on skill than on strength.

How to account for an apparent right bias in structure, when there is no corresponding

bias in the behavioral data from the same species (rhesus macaques, Warren, 1980) or population (Gombe chimpanzees, Marchant and McGrew, 1996)? We suggest that the appropriate variables have yet to be recorded, e.g. the predominant limb providing postural support while arboreal (as hypothesized by Dhall and Singh, 1977; see also MacNeilage et al., 1987).

PRINCIPLES OF LATERALITY

Laterality of function for sagittally paired organs means biased use—a real difference between left and right. (This differs from lateralized use of midline organs, e.g. tongue, or of the whole body, e.g. turning, neither of which is covered here.) However simple the situation, confusion has emerged in terminology; the following gives a simple scheme to clarify matters:

Hand preference is when an individual shows bias on a single task or measure or dependent variable (MacNeilage et al., 1987, p. 248). This is the most basic kind of case study, but is rarely done any more on only a single subject.

Hand specialization is when an individual shows bias across a range of tasks. Ideally, such a battery of measures is exhaustive (includes everything the organism might do with its hands) and exclusive (anything the organism does with its hands falls into only one category). In practice, the range of tasks should be representative of the range of hand function, e.g. from gross to fine motor skill.

Task specialization is when a set of individuals shows a collective bias on a single task. This produces a group or population (or species) effect. This is the most common type of study, usually with a set of subjects picking up small, detached food-items, but it need not generalize to other tasks.

Handedness is thus reserved for when a set of individuals shows a collective bias on a telling battery of tasks (MacNeilage et al., 1987). Thus, the key is the distribution of left-, right-, and non-biased (ambilateral) individuals, with the (usually unstated) expectation of concordance across measures. Such handedness measures are the norm for studies of *Homo sapiens*, usually in the form

of checklists or inventories (McMeekan and Lishman, 1975).

Thus, the ideal study of hand laterality in primates consistently and clearly uses a systematic framework of classification and labelling. Even the simplest criterion, of what constitutes laterality, is made explicit. The ideal study goes beyond “bean-counting” of L’s and R’s to look at function through multiple measures of performance on evolutionarily meaningful tasks.

LEVELS OF LATERALITY

A prerequisite to explaining a phenomenon is being clear about what there is to be explained. As is evident from the above section, even the most basic aspects of laterality of hand function are not yet clear: Are any nonhuman primates surely lateralized? In this sense, hypothetico-deductive models (see above) are premature, or are compromised by circularity, that is, tests of theory-driven predictions are likely to fail, if the predictions are based on faulty findings. Put most starkly, we do not need to explain laterality of hand function if it does not actually exist.

With few exceptions, previous attempts to make sense of the burgeoning literature have ignored or downplayed many methodological issues or have cited selectively from published knowledge. Exhaustive meta-analyses have been done only rarely (e.g. Fagot and Vauclair, 1991; Marchant and McGrew, 1991; Hopkins and Morris, 1993; McGrew and Marchant, 1996, 1997b). More critical synthesis is needed.

Here we provide a simple classificatory framework (not a theoretical model) into which all data on laterality of hand function can be fitted. It is atheoretical and atemporal, and speaks to all three models outlined above (MacNeilage et al. 1987; Warren, 1980; Fagot and Vauclair, 1991), in that it is population-based. Each individual counts as a data-point, classified as one of five types; the set of these points makes a distribution. (For earlier versions of the framework, see McGrew and Marchant, 1996, 1997b.)

Table 1 presents the scheme. Consider an hypothetical population of 20 individual primates, each of which has been measured on a task of laterality. With sufficient data,

TABLE 1. Five levels of laterality of hand function: Hypothetical distribution of 20 individuals

Level	Always Left	Significantly Left	Ambi-Preferent	Significantly Right	Always Right
1	—	—	20	—	—
2	—	10	—	10	—
3	10	—	—	—	10
4a	—	20	—	—	—
b	—	—	—	20	—
5a	20	—	—	—	—
b	—	—	—	—	20

each subject can be classified as: *Always Left*-preferent (uses left hand every time), *Significantly Left*-preferent (uses left hand significantly more often than right hand), *Ambi-preferent* (ratio of left to right hand usages does not differ from 50:50 or random), *Significantly Right*-preferent (uses right hand significantly more than left hand), and *Always Right*-preferent (uses right hand every time). The Binomial test can be used to assign each subject to one of these five categories; thus the scheme includes all subjects measured and not just those that are lateralized.

We consider that five types of distribution are the minimal number needed to illuminate the possibilities raised by current data and theory:

Level 1 is when the majority of individuals are ambipreferent and the minority of individuals are lateralized to either side to varying degrees. Such a population is unlateralized, and in the idealized case, as set out on Table 1, all individuals behave randomly with regard to sagittal bilateral symmetry. (In practice, this is unlikely to occur, if for no other reason than with $\alpha = .05$, 1 in 20 statistical calculations will produce a spurious, false positive result; see above.) Level 1 is assumed to be the baseline condition from which all ontogenetic and phylogenetic biases emerge; it exemplifies the null hypothesis. It is the core of Warren's (1980) model, at least until biasing factors shape individuals to one side or the other.

Level 2 is when most of the subjects are significantly but incompletely (not 100%) lateralized, but their collective distribution to left vs. right does not depart from randomness. In the clearest case, all subjects are lateralized (none is ambipreferent) but not completely so. The population is symmetrical in terms of overall distribution. This corresponds to Fagot and Vauclair's (1991)

low-level handedness (although they did not distinguish between usually and always lateralized subjects). In Warren's (1987) terms, these are individuals who have evolved non-random responding to one side or the other through perseveration or over-practice in unbiased test settings.

Level 3 is when most subjects use only one hand for a task, but their distribution to left vs. right remains random. In the clearest case, all subjects are completely lateralized, that is, exclusively committed to one hand or the other, but the population's distribution remains symmetrical overall. None of the existing models explicitly sets apart such extreme lateralization, but Level 3 can be considered the logical extensions of the states described by Fagot and Vauclair and by Warren for Level 2.

Level 4 is when the majority of individuals are significantly but incompletely lateralized, and when their distribution is significantly skewed to (a) the left, or (b) the right. In the clearest case, all subjects are lateralized to one side or the other. Thus, the overall distribution of individuals in the population is asymmetrical. This corresponds to Fagot and Vauclair's manual specialization for high-level tasks, and to Warren's state in which subjects have been shaped by extrinsic forces to one side or the other. It reflects MacNeilage et al.'s (1987) characterization of population-level left-bias for visually guided reaching and right-bias for skilled object manipulation or for generalized right-handedness.

Level 5 is when the majority of individuals are completely lateralized, and when their distribution is significantly skewed to (a) the left or (b) the right. In the clearest case, all subjects always use the same hand, so the population's distribution is maximally asymmetrical. As with Level 3, none of the existing models remarks on such exclusive

manual commitment, but as Level 3 is the logical extension of Level 2, so Level 5 is the logical extension of Level 4, for all theoretical viewpoints.

(Note that the five-level model is not sequential; it is hard to imagine a five-stage evolutionary progression from Level 1 to Level 5. Instead, from a Level 1 starting point, it is easier to envision two alternative sequences, one that goes to Level 2 and then on to Level 3, or another that goes to Level 4 and then on to Level 5.)

To what extent does reality match this stylized scheme of levels? According to received wisdom in psychobiology, *Homo sapiens* is a Level 5b species: The vast majority of us (ca. 90%) are said to be right-handed for the vast majority of hand usages (Bradshaw and Rogers, 1993; Annett, 1986). This is over simplification, for the latter varies from patterns in which each individual typically uses only one hand for some acts (e.g. handwriting) but uses either hand for others (Marchant and McGrew, 1994; McGrew and Marchant, 1994). Also, such a classification does not take account of cross-cultural differences (Marchant et al., 1995).

The next section presents a comprehensive meta-analysis that seeks to classify all published data on hand laterality in nonhuman primates into this five-level framework, providing certain criteria of quality control are met by the data-sets.

RESULTS OF META-ANALYSIS

The following criteria were set for inclusion of a data-set in the meta-analysis, based on the issues raised above:

- 1) Explicit safeguard (of any sort) that seeks to ensure *independence of data-points* vs. absence of any such safeguard;
- 2) Majority of subjects apparently *adults* vs. only minority of adults;
- 3) Enough ($N \geq 6$) data-points per subject to allow subject to be categorized as *lateralized* by Binomial test (two-tailed, $P < .05$) or its equivalent vs. fewer data-points;
- 4) Sufficiently specifically-defined and ecologically valid *behavioral category* (task) vs. general (e.g. touch self) or artificial (e.g. handle joystick) categories;

- 5) Raw or derived data provided to allow subject to be *classed* as AL, SL, A, SR, or AR vs. absent or transformed data not amenable to this operation;
- 6) *Species* of subject vs. imprecise (e.g. monkey) or general (e.g. macaque) identification;
- 7) *Number* of subjects in population is six or greater vs. five or fewer, thus allowing binomial testing of distribution of individuals in the population.

No selective criteria were imposed on the grounds of sex, kinship, setting, or number of tasks.

A total of 241 data-sets were scrutinized, of which 193 were rejected on one or more criteria as listed above. (A complete listing of the 241 studies, plus the grounds for omission or inclusion for each, is available from the authors.)

Prosimians

We found 24 published studies of Strepsirrhini that had data on behavioral laterality of hand use. (Remarkably 16 of 24 came from one prolific research group, that of Ward, 1995, 1997b and her colleagues, who have studied both African and Malagasy, nocturnal and diurnal prosimians.) Of these, 12 met all seven criteria as detailed in the previous section; of these the most frequent problems were low sample sizes of subjects or lack of individually reported data. Of the Lemuriformes, five families (Indriidae, Daubentoniidae, Lemuridae, Cheirogaleidae, Galagidae) but not Lepilemuridae were tested; we found no studies of Tarsiiformes. Table 2 lists the 12 studies of nine species by task and by distribution of individuals, cast in five levels or types of laterality of hand function, as outlined above.

Only two studies showed ambilaterality to be predominant, and both yielded observational data on species-typical foraging activities by aye-ayes (*Daubentonia madagascariensis*, Feistner et al., 1994) and gentle lemurs (*Hapalemur griseus*, Stafford et al., 1993). Although they were partly lateralized individually (Level 2), these two specialist food-processors showed less marked lateralization than other species of prosimians.

The overwhelming consensus for strepsirrhine hand function was significant but in-

TABLE 2. Hand laterality in prosimians: Distribution of individuals, by species and task, over levels of laterality

Level	Species	Task	Distribution of individuals						Source
			N	AL	SL	A	SR	AR	
1	<i>Daubentonia madagascariensis</i>	Tap object (forage)	11	—	3	6	2	—	Feistner et al., 1994
2	<i>Haplemur griseus</i>	Feed with long finger	11	—	2	6	3	—	Stafford et al., 1993
	<i>D. madagascariensis</i>	Grasp and pull stalk	11	—	3	8	—	—	
	<i>H. griseus</i>	Hold object	11	—	3	5	3	—	Feistner et al., 1994
		Pull stalk (food proc.)	11	—	3	4	4	—	Stafford et al., 1993
		Rotate stalk (food proc.)	11	—	7	2	2	—	
		Feed in (ingest) stalk	11	—	7	2	2	—	Mason et al., 1995
	<i>Propithecus verreauxi</i>	Take food from mouth	15	—	6	5	4	—	
	<i>Otolemur garnetti</i>	Hold food	23	—	6	9	8	—	Milliken et al., 1991
		Manipulate food	23	—	7	9	7	—	
		Take food from cup	23	1	6	3	13	—	Forsythe and Ward, 1988
	<i>Lemur macaco</i>	Take food from pan	33	1	19	1	12	—	
	<i>Microcebus murinus</i>	Take food from cup (half bip.)	8	—	3	1	4	—	Dodson et al., 1992
	<i>Galago moholi</i>	Take food from tube (half bip.)	16	1	4	0	11	—	
3	<i>G. senegalensis</i>	Take food from cup (half bip.)	10	—	7	—	3	—	Larson et al., 1989
	<i>L. catta</i>	Take/pick up food	21	2	7	3	8	—	
	<i>L. catta</i>	Hold/eat chow	21	4	5	2	10	—	Bennett et al., 1995
		Hold/eat fruit	21	6	4	3	6	2	
	<i>L. catta</i>	Take food from box	13	3	4	3	—	3	Milliken et al., 1989
		Pick up and peel food	13	5	2	4	2	—	
	<i>H. griseus</i>	Take food from dish	13	6	2	—	2	3	Stafford et al., 1993
4	<i>G. senegalensis</i>	Take food from rod	8	—	7	1	—	—	Sanford and Ward, 1986

N = number of subjects; AL = Always Left = uses left hand 100%; SL = Significantly Left = uses left hand significantly more often; A = Ambilateral = uses each hand equally often; SR = Significantly Right = uses right hand significantly more often; AR = Always Right = uses right hand 100%.

Bold-face numbers refer to predominant categories (see text). For explanation of levels, see text.

complete lateralization on an individual basis, but symmetrical distribution for the population, i.e. Level 2. However, all measures had to do with food, either acquiring or processing it, usually by taking it from a container, so the extent to which these data generalize to other acts is yet unknown. Species differences emerged. Because Coquerel's sifaka acquires food by mouth, the measure for hand laterality had to be taking food from the mouth for handling, rather than putting food to the mouth (Mason et al., 1995). Two studies elicited bipedal performance in taking food from a container but got different results: Larson et al. (1989) found for 10 lesser bushbabies (*Galago senegalensis*) that bipedal posture facilitated use of the dominant hand, but Dodson et al. (1992) found that induced postural adjustments had no effect on hand laterality in 16 galagos (*G. moholi*) or eight mouse lemurs (*Microcebus murinus*).

Multiple studies of the ringtailed lemur (*Lemur catta*) raise the possibility of inter-

population differences. Three studies done at the Duke University Primate Center show the species to be consistently at Level 2, with a few individuals lateralized completely to the left (Bennett et al., 1995; Ward, 1995; Ward et al., 1990). But a family of 13 *Lemur catta* in the Memphis Zoo showed no clear distribution of individuals (Milliken et al., 1989).

The single Level 3 result, in which most individuals used only one hand or the other, was notable and aberrant (see above): nine of 13 gentle lemurs were completely lateralized for the simple reaching task of taking food from a dish, while the same individuals were far less lateralized for food processing (Stafford et al., 1993).

The only result leading to population-level but partial laterality (Level 4) was of eight lesser bushbabies being offered (live?) mealworms on the end of a rod; seven individuals took the prey significantly more often with their left hands (Sanford and Ward, 1986).

We found no data at Level 5 for any strepsirrhine primates, i.e. no population in which most individuals were 100% committed to the same hand.

Overwhelmingly, at least for the limited range of food handling tasks so far studied, prosimians show Level 2 laterality. In any given population, most individuals are significantly but incompletely committed to one hand or the other, but the population as a whole remains symmetrically distributed (cf. Bishop, 1964; Ward, 1995).

New World monkeys

We found 43 studies of Haplorrhini that provided published data on behavioral laterality of hand use. Of these, only 19 met all seven criteria as outlined above; the most frequent problems that led to omission were lack of evidence of independent data points and lack of raw data to allow classification of individuals. These 19 studies were of only six species: Cebidae (*Cebus apella*, *C. capucinus*, *Saimiri sciureus*, *Ateles geoffroyi*) and Callitrichidae (*Callithrix jacchus*, *Saguinus oedipus*). Table 3 gives the results in terms of the five-level framework.

Few findings were at Level 1, ambilaterality, but almost all had to do with spontaneous, everyday activities, especially from a quadrupedal posture. The only field study of laterality, Panger's (1997) of white-faced capuchins in Costa Rica, featured most prominently, reiterating the need for normative studies of primate laterality in nature. Cottontop tamarins (*Saguinus oedipus*) observed ethologically in a naturalistic captive colony were unlateralized for various habitual acts, especially self-maintenance (Diamond and McGrew, 1994).

The majority of studies examined were at Level 2 and involved manipulating food items or acquiring them from demanding circumstances. The more challenging acquisitions entailed varieties of extraction of embedded or elusive food-items, or of elicited, unusual postures, usually hanging vertically or assisted bipedalism. In three studies (capuchins, Anderson et al., 1996; capuchins, Parr et al., 1997; squirrel monkeys, Laska, 1996a) monkeys went from Level 1 to Level 2 when they changed from

quadrupedal foraging on the ground to elevated, more complex tasks requiring postural reconfiguration. Such individual lateralization also included most cases of tool-use, all by *Cebus apella*: probing for honey (Anderson et al., 1996); sponging juice from a container (Westergaard and Suomi, 1993a) and hammering nuts with a stone (Westergaard and Suomi, 1993b). A few tasks showed indications of more complete lateralization by individuals, e.g. picking up fast-moving items (common marmosets, Hook-Costigan and Rogers, 1995) or pounding or rubbing objects on the substrate (Panger, 1997), but in both studies the number of subjects was small.

Only two studies recorded Level 3 findings in which most individuals used only one hand or the other to do a task. Most (eight of 13) tufted capuchins used one hand to extract strawberry syrup from an elevated tube that had to be climbed to be used (Anderson et al., 1996). In another population of the same species, 10 of 13 subjects used metal bolts as probes to dip out syrup from a tube (Westergaard and Suomi, 1994; see also Westergaard et al., 1997b). There is no obvious difference between these tasks and several of those listed above in Table 2 as Level 2 tasks.

Tasks that achieve Level 4 status were heterogeneous. Some studies involved haptic tasks, that is, cases where the monkey had to extract an invisible food item, sometimes from a matrix, using the sense of touch for guidance (spider monkeys, Laska, 1996b; brown capuchin monkeys, Parr et al., 1997). Other studies involved merely picking up food-items, but while in a bipedal posture. The only study that entailed making and using stone tools, i.e. a cutting edge to cut through a barrier, also falls here (tufted capuchins, Westergaard and Suomi, 1996a). Laska's (1996b) is the only published study of laterality in ateline monkeys, who are notably characterized by lacking a thumb; whether this morphological constraint elicits tendencies toward population level asymmetry awaits further study. Finally, the biases in the distribution of individuals at Level 4 are to either side; there is

TABLE 3. Hand laterality in New World monkeys: Distribution of individuals, by species and task, over levels of laterality

Level	Species	Task	N	Distribution of individuals					Source
				AL	SL	A	SR	AR	
1	<i>Saguinus oedipus</i>	Social groom	15	—	—	8	7	—	Diamond and McGrew, 1994 ^a
		Self-groom	8	—	—	8	—	—	
		Scratch self	20	—	1	18	1	—	
		Hit another	18	—	—	15	3	—	
		Carry object	11	—	—	7	2	2	
	<i>Cebus capucinus</i>	Pick (up) food	51	—	2	45	4	—	Panger, 1997 ^a
		Tap object (forage)	10	—	—	10	—	—	
		Pick up food	14	—	—	11	3	—	
		Carry object	14	—	—	12	2	—	
		Touch self	35	—	—	32	3	—	
	<i>C. apella</i>	Pick up food	22	—	4	15	3	—	Westergaard et al., 1997b ^a
	<i>S. oedipus</i>	One-arm vert. suspension	28	—	9	13	6	—	Parr et al., 1997 ^a
	<i>C. apella</i>	Pick up food	13	—	2	8	3	—	King, 1995 ^a
	<i>C. apella</i>	Pick out food	35	—	3	22	10	—	Anderson et al., 1996 ^a
	<i>Saimiri sciureus</i>	Touch own face	9	—	—	8	1	—	Westergaard et al., 1997b ^a
		Scratch own body	13	—	—	11	2	—	
	<i>S. sciureus</i>	Pick up food	12	—	3	6	3	—	Aruguete et al., 1992 ^a
	2	<i>S. oedipus</i>	Spont. grasp object	30	—	5	13	12	Laska, 1996a ^a
		<i>C. apella</i>	Pick up food	28	—	8	13	7	King, 1995 ^a
	<i>S. oedipus</i>	Take food (quad.)	14	—	5	4	5	—	Westergaard et al., 1997c ^a
	<i>Callithrix jacchus</i>	Take food while vert. cling	14	—	4	2	8	—	Roney and King, 1993 ^a
		Hold/eat food	17	—	9	2	6	—	
	<i>S. oedipus</i>	Take food while suspended	20	—	10	5	5	—	Hook-Costigan and Rogers, 1998 ^a
	<i>C. jacchus</i>	Hold/eat food	8	—	2	2	4	—	King, 1995 ^a
		Pick up slow-moving food	8	—	2	1	5	—	
	<i>C. apella</i>	Take food through hole	8	—	6	1	1	—	Hook-Costigan and Rogers, 1995
		Hang and pick up food	13	—	3	6	4	—	
		Take food from tube	13	—	6	3	4	—	
		Probe for honey (tool)	10	—	5	1	4	—	
		Probe for honey (bipedal)	10	—	6	1	3	—	
	<i>C. apella</i>	Take liquid from tube	13	—	6	1	4	2	Anderson et al., 1996 ^a
		Take food from tube (bip.)	13	—	6	1	5	1	
		Take food from container	21	2	6	1	9	3	
		"Sponge" up juice (tool)	14	1	4	2	5	2	
		Hammer nuts (tool)	14	1	7	2	3	1	
	<i>S. sciureus</i>	Take food from ring (bip.)	12	1	5	2	4	—	Westergaard and Suomi, 1993b
		Take hidden food (bip.)	12	1	4	1	6	—	
	<i>S. sciureus</i>	Take food from tube (bip.)	12	2	4	—	3	3	Laska, 1996a ^a
		Take food (quad.)	30	—	12	5	13	—	
	<i>S. sciureus</i>	Take food while vert. cling	30	1	15	—	14	—	Roney and King, 1993 ^a
		Take food while vert. cling	16	—	3	3	9	1	
	<i>S. sciureus</i>	Take food from slot (quad.)	30	—	10	5	14	1	King and Landau, 1993 ^a
		Take food from slot (bip.)	30	2	7	8	12	1	
	<i>C. apella</i>	Take food from pipe	34	1	13	5	11	4	Westergaard and Suomi, 1996c ^a
	<i>C. apella</i>	Take food from tube	44	5	12	9	14	4	Westergaard and Suomi, 1996b ^a
	<i>C. apella</i>	Take food from basket (bip.)	22	—	10	9	3	—	Parr et al., 1997 ^a
	<i>S. sciureus</i>	Take hidden food from box	22	—	9	11	2	—	Aruguete et al., 1992 ^a
		Touch environment	13	—	7	—	6	—	
	<i>C. jacchus</i>	Hang and pick up food	8	2	1	2	3	—	Hook-Costigan and Rogers, 1995
		Grasp swinging object	8	2	1	2	3	—	
	<i>C. capucinus</i>	Pick up fast-moving food	8	3	—	2	3	—	Panger, 1997 ^a
		Non-food object on substrate	6	1	1	1	1	2	
	<i>S. oedipus</i>	Take food from moving platform	22	2	7	5	6	2	King, 1995 ^a
	3	<i>C. apella</i>	Take food from static platf.	22	3	7	2	6	Anderson et al., 1996 ^a
		<i>C. apella</i>	Take liquid from tube (bip.)	13	3	3	1	5	
	<i>C. apella</i>	Probe liquid from tube (tool)	13	7	1	—	2	3	Westergaard and Suomi, 1994
	<i>C. apella</i>	Probe liquid from tube (tool)	18	1	6	2	1	8	Westergaard and Suomi, 1997
	4	<i>C. apella</i>	Cut barrier with stone (tool)	6	—	—	4	2	Westergaard and Suomi, 1996a
		Strike stone on substrate	14	—	1	4	9	—	
	<i>C. apella</i>	Pick up food (bipedal)	28	—	6	5	16	1	Westergaard et al., 1997c ^a
	<i>S. oedipus</i>	Hold object	20	—	—	6	14	—	Diamond and McGrew, 1994 ^a
		Pick up object	20	—	—	5	14	1	
	<i>S. sciureus</i>	Grasp fish in bowl	16	—	11	2	2	1	King and Landau, 1993 ^a
		Grasp fish in pool	12	—	9	3	—	—	
	<i>C. apella</i>	Take hidden, matrixed food	22	—	13	6	3	—	Parr et al., 1997 ^a
		Take hidden food from water	22	—	15	2	5	—	
	<i>Ateles geoffroyi</i>	Pick up food	13	3	6	3	—	1	Laska, 1996b ^a
		Pick up food (bipedal)	13	1	9	2	—	1	
		Take hidden food (bip.)	13	3	8	—	1	1	

N = number of subjects; AL = Always Left = uses left hand 100%; SL = Significantly Left = uses left hand significantly more often; A = Ambilateral = uses each hand equally often; SR = Significantly Right = uses right hand significantly more often; AR = Always Right = uses right hand 100%.

^a Supplementary data supplied by authors.

Bold-face numbers refer to predominant categories (see text). For explanation of levels, see text.

no consensus across results to either Level 4a (left) or 4b (right).

We found no evidence of Level 5 performance, i.e. population-level, exclusively one-sided hand use, in haplorhine monkeys.

As for prosimians, most studies of New World monkeys showed Level 2 results, with the majority of subjects individually (but not completely) lateralized for a given task (cf. Hook-Costigan and Rogers, 1997). Unlike prosimians, New World monkeys showed much more heterogeneity, especially over Levels 1 and 4, although fewer species (six vs. nine) were studied.

Old World monkeys

For catarrhine monkeys, 90 studies with data on hand laterality were found and scrutinized. Most were laboratory studies of macaques (*Macaca* spp.) and 51 were published before 1987, making them on average much older than studies of other taxa. Moreover, 31 publications came from just three research groups, those of Ettlinger (e.g. 1988), Lehman (e.g. 1993) and Warren (e.g. 1980). All of these laboratories were paradigmatically committed to blocked training and testing of large numbers of subjects in rigorous experimental settings, often on some variant of the Wisconsin General Test Apparatus (WGTA). Only one "modern" research group on Old World monkeys rivals this concentration, that of Vauclair and Fagot (1993), working primarily on Guinea baboons (*Papio papio*), but also on other species and in various settings.

Few studies fulfilled the criteria set out above; only seven met all 11 criteria. Several older studies did not even specify the species being studied, and many tested only (more tractable?) immature subjects. Many provided only summary statistics for the group as a whole, instead of supplying individual data, but the most common problem in more than two-thirds of reports was the lack of any mention of attention to independence of data points. With blocks of many repetitive trials that could lead to inflated N's for statistical testing, this raised genuine problems. (It might be argued that the standard WGTA protocols ensure independence of each trial, e.g. when the vertical panel descends to shield the experimenter's rebaiting of the

food-well, but this says nothing about the monkey's behavior. The subject may sit still with hand poised for the next response throughout the predictable, stereotyped sequence.) Finally, many studies of the neuropsychology of hand laterality in rhesus macaques (*Macaca mulatta*) involved the training of hand preferences in subjects, often prior to selective cerebral ablation (e.g. Ettlinger et al., 1968); such data are hard to classify in the present framework, although no study was omitted on the grounds of the fourth criteria alone.

The seven studies that met all criteria were atypical, not only for Old World monkeys, but for all studies of hand laterality in primates. Four were of wild populations, plus two in seminatural, large enclosures (Fagot et al., 1991; Vauclair and Fagot, 1987a), leaving only two done in traditional test settings (Westergaard and Suomi, 1996b; Rigamonti et al., 1997). (See Table 4.)

Level 1 results are the most common: Mittra et al. (1997) found wild common langurs (*Presbytis entellus*) in a Nepalese forest to be unlateralized on a range of social and maintenance activities. Vauclair and Fagot (1987a) combined all hand movements into a single category in observations of enclosure-living Guinea baboons, *Papio papio*; most were unlateralized. Wild but provisioned Japanese macaques (*Macaca fuscata*) on Koshima Island carried sweet potatoes to the water for washing; most were unlateralized for the task (Watanabe and Kawai, 1993). The same monkeys were also mostly unlateralized for picking up food from the ground (Tokuda, 1969).

Level 2 laterality appears in the Koshima Island monkeys for the more challenging task of carrying handfuls of wheat grains (Watanabe and Kawai, 1993), and in extractive foraging: Taking tiny, embedded food pellets from a matrix by captive pigtailed macaques (*M. nemestrina*) (Rigamonti et al., 1997) and taking food from a tube by rhesus macaques (Westergaard and Suomi, 1996a). However, it also emerged for the simple task of picking up grain from the ground by Guinea baboons (Vauclair and Fagot, 1987b).

Only two Level 3 results emerged: In arguably the most skillful motor task shown by free-ranging primates, most Koshima

TABLE 4. Hand laterality in Old World monkeys: Distribution of individuals, by species and task, over levels of laterality

Level	Species	Task	N	Distribution of individuals					Source
				AL	SL	A	SR	AR	
1	<i>Presbytis entellus</i>	Idle (inactive)	10	—	—	10	—	—	Mittra et al., 1997 ^a
		Grasp and retrieve object	10	—	1	9	—	—	
		Hold object	10	—	1	8	1	—	
		Groom self	8	—	—	7	1	—	
		Groom another	6	—	—	5	1	—	
	<i>Papio papio</i>	Pick up and eat food	10	—	3	6	1	—	Vauclair and Fagot, 1987a Watanabe and Kawai, 1993
		All free hand movements	18	—	2	11	5	—	
		Carry sweet potatoes	26	1	3	22	—	—	
		Pick up food from ground	41	4	5	29	2	1	
		Social groom	108	4	15	74	14	1	
2	<i>Macaca fuscata</i>	Pick up food (bipedal)	27	—	9	7	11	1	Westergaard et al., 1997a ^a
	<i>M. fuscata</i>	Carry wheat grains	15	—	8	1	6	—	Watanabe and Kawai, 1993
	<i>M. nemestrina</i>	Extract food from hole	10	—	2	3	4	1	Rigamonti et al., 1997 ^a
	<i>M. mulatta</i>	Take food from tube	55	3	11	15	22	4	Westergaard and Suomi, 1996a ^a
	<i>P. papio</i>	Pick up food	11	—	2	2	6	1	Vauclair and Fagot, 1987b ^a
	<i>M. fuscata</i>	Catch thrown sweet potato	24	9	—	11	—	4	Kawai, 1967
3	<i>M. mulatta</i>	Joystick controls cursor	35	14	—	—	—	21	Hopkins et al., 1992 ^a
	<i>M. mulatta</i>	Pick up food (quadrupedal)	28	2	14	8	4	—	Westergaard et al., 1997a ^a
	<i>M. mulatta</i>	Take food from matrix in box while hanging tripedally	29	1	20	4	4	—	Fagot et al., 1991

N = number of subjects; AL = Always Left = uses left hand 100%; SL = Significantly Left = uses left hand significantly more often; A = Ambilateral = uses each hand equally often; SR = Significantly Right = uses right hand significantly more often; AR = Always Right = uses right hand 100%.

^a Supplementary data supplied by authors.

Bold-face numbers refer to predominant categories (see text). For explanation of levels, see text.

Island monkeys used one hand exclusively to catch on the fly, sweet potatoes thrown to them (Kawai, 1967). The remainder mostly used both hands. Similarly demanding was an artificial task in which rhesus macaques used a joystick to control an on-screen cursor—every one of 35 individuals used only one hand to do so (Hopkins et al., 1992).

Level 4a laterality predominated in an artificial foraging task requiring touch rather than vision: rhesus macaques reached with left hands into a box to extract peanuts from sand and pebbles, while hanging from the mesh of an outdoor enclosure (Fagot et al., 1991). Bafflingly, it also emerged in simple reaching by rhesus monkeys to pick up food items from the floor (Westergaard et al., 1997a).

In summary, as with New World monkeys, Old World monkeys showed increased individual laterality with increased demands on the motor skills of handling objects, but the only population level result emerged from another sensory modality, when haptic rather than visual stimuli informed the working hand.

Apes

Studies of hand laterality in apes have risen dramatically in the last decade: 67%

(58 of 86) studies have been published since 1987. Many were directly stimulated by MacNeilage et al.'s (1987) pointing out that apes had been largely ignored in hand laterality research.

Of the 86 published data papers, 18 met the criteria for coding in the meta-analysis. By far the biggest problem was in the seventh criterion, in that 40 studies lacked the minimum of six or more subjects. The second most common problem, mostly in older research, was no mention of taking steps to ensure the independence of data points (Shaffer, 1997). All genera of apes were coded, but some species of gibbons (*Hylobates* spp.) have yet to be studied. Chimpanzees (*Pan troglodytes*) represent almost half of the data sets, so they are presented in a separate table (Table 6). Since on average fewer apes than monkeys are found in laboratories, the ape data present a higher proportion of studies of free-ranging subjects than do the other taxa.

Table 5 gives the distribution of individuals by task for three species of lesser apes (*Hylobates concolor*; *H. lar*; *H. syndactylus*) and four types of great apes (lowland gorilla, *Gorilla g. gorilla*; mountain gorilla, *G.g.*

TABLE 5. Hand laterality of apes (except chimpanzee): Distribution of individuals, by species and task, over levels of laterality

Level	Species	Task	Distribution of individuals						Source
			N	AL	SL	A	SR	AR	
1	<i>Hylobates syndactylus</i>	Pick up food or object (precision)	13	—	—	13	—	—	Heestand, 1986
		Pick up food or object (power)	13	—	—	12	1	—	
		Hang suspended by arm	13	—	2	9	2	—	
	<i>Gorilla g. gorilla</i>	Leading arm in climb	13	—	—	7	6	—	
		Pick up food or object (precision)	29	—	2	23	4	—	
		Pick up food or object (power)	29	—	1	25	3	—	
	<i>Pongo pygmaeus</i>	Leading arm in climb	29	—	1	20	4	—	
		Pick up food or object (precision)	8	—	—	7	1	—	
		Pick up food or object (power)	8	—	—	8	—	—	
	<i>Pan paniscus</i>	Leading arm in climb	8	—	—	8	—	—	Hopkins et al., 1993c
		Carry food, object or infant	11	—	2	9	—	—	
		Touch own head or face	11	—	1	9	1	—	
	<i>P. paniscus</i>	Touch own body	10	—	2	8	—	—	Hopkins and deWaal, 1995 ^a
		Communicative gesture	9	—	1	6	2	—	
		Grasp food	11	—	1	8	2	—	
		Leading arm in locomotion	11	—	—	6	5	—	
		Carry food, object or infant	10	—	4	6	—	—	
		Touch own head or face	10	—	2	8	—	—	
		Touch own body	10	—	—	8	2	—	
2	<i>G.g. beringei</i>	Pick up food	10	—	1	9	—	—	Schaller, 1963
		Leading arm in locomotion	10	—	—	3	7	—	
		Chest beat	6	—	—	4	2	—	
	<i>H. concolor</i>	Pick up food	7	—	—	1	3	3	Stafford et al., 1990
		Pick up food	8	—	—	2	3	3	
	<i>H. syndactylus</i>	Pick up food	12	—	—	3	5	4	Olson et al., 1990
		Pick off food from mesh	12	—	—	3	5	4	
	<i>P. pygmaeus</i>	Pick up food	12	—	—	2	5	5	
		Pick up food	8	—	—	6	—	2	
	<i>G.g. gorilla</i>	Pick up food (quadrupedal)	9	—	—	3	4	2	Hopkins, 1993
		Pick up food (upright)	8	—	—	1	3	4	
	<i>H. lar</i>	Pick up food	10	—	—	3	4	3	Fagot and Vaclair, 1988a
		Leading arm in brachiation	11	—	—	5	4	2	
	<i>P. pygmaeus</i>	Leading arm in walk-run	8	—	—	—	7	—	Heestand, 1986
		Process nettle	38	1	—	9	10	16	
	<i>G.g. beringei</i>	Procure <i>Galium</i>	38	—	—	20	5	13	Byrne and Byrne, 1993
		Accumulate <i>Galium</i>	38	2	—	19	4	12	
		Hold nettle	38	3	—	11	3	19	
		Eat <i>Galium</i>	38	7	—	16	2	12	
		Process <i>Galium</i>	38	8	—	13	3	13	Byrne and Byrne, 1991
		Eat nettle	38	11	—	1	7	8	
3	<i>G.g. beringei</i>	Process celery	38	11	7	5	3	12	Byrne and Byrne, 1991
		Process nettle	36	12	7	4	4	9	
4	<i>G.g. gorilla</i>	Pick off food from mesh	12	—	2	—	10	—	Olson et al., 1990
		Pick off food from mesh	6	—	—	6	—	—	
	<i>H. lar</i>	Leading arm in walk-run	13	—	1	3	9	—	Heestand, 1986
5	<i>G.g. gorilla</i>	Leading arm in walk-run	29	—	—	2	8	19	
		Extract food-sliding panel	8	5	2	—	1	—	
	<i>G.g. beringei</i>	Process thistle leaf (fine manip.)	33	5	6	4	2	16	Byrne and Byrne, 1991

N = number of subjects; AL = Always Left = uses left hand 100%; SL = Significantly Left = uses left hand significantly more often; A = Ambilateral = uses each hand equally often; SR = Significantly Right = uses right hand significantly more often; AR = Always Right = uses right hand 100%.

^a Supplementary data supplied by authors.

Bold-face numbers refer to predominant categories (see text). For explanation of levels, see text.

beringei; bonobo or pygmy chimpanzee, *Pan paniscus*; orangutan, *Pongo pygmaeus*).

Most activities at Level 1 were either simple picking up of food or basic positional

or postural behavior (Heestand, 1986). Both studies of bonobos also fall here, for a variety of tasks, including gestures of communication (Hopkins et al., 1993c; Hopkins and

de Waal, 1995). The first field data on hand laterality came from Schaller (1963) on chest-beating in male displays; although only two of eight individuals were significantly lateralized, all eight more often started their displays with the right hand (binomial, $N = 8$, $x = 0$, $P = .008$).

Most Level 2 findings are of picking up food, usually from the substrate, but from relatively small samples of populations (Stafford et al., 1990; Olson et al., 1990; Hopkins, 1993; Fagot and Vauclair, 1988a). However, Byrne and Byrne's (1991, 1993) monumental study of mountain gorillas processing terrestrial herbaceous vegetation for food also mostly sits here.

However, such food processing gradates into Level 3 for two of those foods, nettle and wild celery. All of these tasks were sequentially contingent and bimanual, as the gorillas transformed the plant-parts to circumvent the mechanical defenses of the foliage.

The two activities that show partial lateralization on a population scale (Level 4) were very different: Both white-handed gibbons and lowland gorillas tended to lead off bouts of quadrupedal locomotion with the right hand (Heestand, 1986). The same two species showed lateralization for a form of extractive foraging in captivity—picking off raisins affixed to cage mesh (Olson et al., 1990)—though they favored opposite hands to do so.

Only one clear Level 5 result emerged: in bimanual processing of spiny thistle leaves, 16 of 33 mountain gorillas used only their right hands to do the fine manipulation (Byrne and Byrne, 1991). Interestingly, an elegant but artificial bimanual task, sliding a panel to give access to a food-item, showed a similar pattern: five of eight captive lowland gorillas used only their left hand (Fagot and Vauclair, 1988a).

In summary, although the bulk of data from apes resembles that of other nonhuman primates in being Level 1 or 2, there are intriguing signs of population level laterality at Levels 4 and 5, although not in the same direction. Notably near-absent are data at Level 3, the most extreme form of individual lateralization.

Chimpanzees

Pan troglodytes is unusual in that more studies of hand laterality have been done in nature than for any other species of nonhuman primate. There are published data from Gombe (Marchant and McGrew, 1996) and Mahale (Nishida, 1973; Nishida and Hiraiwa, 1982) in Tanzania, Bossou in Guinea (Sugiyama et al., 1993; Matsuzawa, 1994, 1996), and Tai in Ivory Coast (Boesch, 1991). (In contrast, there are no published data on hand laterality in wild bonobos, orangutans or lowland gorillas.) Chimpanzees are second only to rhesus monkeys in the number of studies done on hand laterality in nonhuman primates. More than a third (23 of 62) of these studies of *Pan troglodytes* have been by Hopkins (1996) and his colleagues, working with the large captive colony at the Yerkes Primate Research Center.

Most everyday, simple activities in free-ranging or semi-free-ranging (e.g. outdoor enclosures) chimpanzees are remarkably unlateralized (see Table 6). Gombe's apes lead largely 50:50 lives, in terms of subsistence, self-maintenance, or socializing (Marchant and McGrew, 1996). Similar results held for zoos (Heestand, 1986; Steiner, 1990), and for chimpanzees on naturalistic islands (Marchant, 1983). Picking (up) food, whether attached (Sugiyama et al., 1993) or detached (Boesch, 1991; Tonooka and Matsuzawa, 1995) is split between Levels 1 and 2 (see below). The most marginal activity is the only tool use that qualifies as Level 1, throwing (Marchant, 1983), and it falls halfway between Levels 1 and 2.

At Level 2, apart from more data on picking up food (Hopkins, 1993; Colell et al., 1995a), the other two data-sets involved the manipulation of objects (Marchant, 1983; Steiner, 1990). An extensive data-set ($N = 36$ individuals) on throwing sits just on the borderline between Levels 2 and 3: About half of the lateralized subjects are incompletely so, and half are completely committed to one hand or the other (Hopkins et al., 1993b).

All data of Level 3 lateralization concern tool use by wild chimpanzees: using sticks or stones to crack open nuts on root or stone

TABLE 6. *Hand laterality of chimpanzees: Distribution of individuals, by setting and task, over levels of laterality*

Level	Setting	Task	N	Distribution of individuals					Source
				AL	SL	A	SR	AR	
1	Wild	Pluck attached food	32	—	—	32	—	—	Marchant and McGrew, 1996 ^a
		Scratch self	36	—	1	34	1	—	
		Eat	35	—	1	31	3	—	
	Zoos	Social groom	31	—	1	28	2	—	Heestand, 1986
		Pick up food/object (precision)	20	—	1	17	2	—	
		Pick up food/object (power)	20	—	3	15	2	—	
		Leading arm in climb	20	—	—	14	6	—	
	Island	Social groom	20	—	2	17	1	—	Marchant, 1983
		Pick up and hold object	26	—	4	21	1	—	
		Carry object	26	—	7	15	4	—	
		Pick up and eat food	26	—	9	13	4	—	
	Wild	Pick attached food	19	—	1	18	—	—	Sugiyama et al., 1993
		Pick up food	20	1	2	13	3	1	
	Zoo	Social groom	15	—	—	10	4	1	Boesch, 1991
		Groom self	6	—	1	5	—	—	
		Eat by hand	6	—	2	4	—	—	
	Caged	Hold object or other	7	—	2	4	1	—	Steiner, 1990
		Touch own body	26	—	3	20	3	—	
		Touch own face	25	—	5	18	2	—	
		Touch environment	25	—	1	14	10	—	
	Lab/Zoo	Pick up food	80	2	20	42	16	—	Tonooka and Matsuzawa, 1995
	2	Island	Throw (tool)	18	—	4	9	5	—
Lab		Pick up food (quadrupedal)	40	—	11	20	9	—	Hopkins, 1993
Zoo		Manipulate object	7	—	4	1	2	—	Steiner, 1990
Island		Pick up/touch food/object/other	26	—	11	5	10	—	Marchant, 1983
Zoos		Pick up food	31	—	10	6	15	—	Colell et al., 1995a
Lab		Throw (tool)	36	5	4	6	12	9	Hopkins et al., 1993b ^a
Island		Pick up/touch food/object/other	26	—	11	5	10	—	Marchant, 1983
3	Zoos	Pick up food	31	—	10	6	15	—	Colell et al., 1995a
	Lab	Throw (tool)	36	5	4	6	12	9	Hopkins et al., 1993b ^a
	Wild	Hammer nuts (tool)	41	8	10	5	8	10	Boesch, 1991
		Dip wadge (tool)	16	3	1	3	0	9	
	Wild	Crack fruit on anvil	14	4	1	2	2	5	McGrew et al., 1997 ^a
	Wild	Hammer nuts (tool)	13	5	—	1	2	5	Sugiyama et al., 1993
4	Wild	Fish for termites (tool)	36	12	4	9	5	6	McGrew and Marchant, 1996 ^a
	Zoos	Drink from hand	9	1	—	—	4	4	Colell et al., 1995a
		Make waves with hand	8	1	—	—	4	3	
	Zoos	Leading arm in walk-run	20	—	4	3	13	—	Heestand, 1986
	Lab	Eat while holding food	140	—	25	66	49	—	Hopkins, 1994 ^a
	Lab	Pick up food (upright)	40	—	5	13	22	—	Hopkins, 1993

N = number of subjects; AL = Always Left = uses left hand 100%; SL = Significantly Left = uses left hand significantly more often; A = Ambilateral = uses each hand equally often; SR = Significantly Right = uses right hand significantly more often; AR = Always Right = uses right hand 100%.

^a Supplementary data supplied by authors.

Bold-face numbers refer to predominant categories (see text). For explanation of levels, see text.

anvils (Boesch, 1991; Sugiyama et al., 1993); using fruit fibre as a wadge to sponge up water (Boesch, 1991); using flexible probes of vegetation (bark, grass, twig, vine, etc.) to "fish" termites from their earthen mounds (McGrew and Marchant, 1996); using stones or roots as anvils to smash open hard-shelled fruits (McGrew et al., 1997). Level 3 is important: chimpanzees committed to only one hand (i.e. AL or AR) in termite fishing are more efficient than others who use either hand (i.e. SL, A, SR) (McGrew and Marchant, 1997a).

Level 4 data are much more heterogeneous: like the other apes (see above), chimpanzees led off bouts of locomotion with their right arms (Heestand, 1986). Colell et al. (1995a) found right-sided tendencies in two unusual patterns showed by Barcelona Zoo apes living in a water-moated enclosure: they scooped up drinking water in a cupped hand and they made currents in the water to retrieve floating objects. Hopkins (1993) showed that upright chimpanzees picking up food were lateralized to the right, while the same individuals showed no population-

level tendencies when quadrupedal. In a sample of 140 apes eating with one hand while the other hand held food, twice as many (49 vs. 25) were lateralized to the right as to the left (Hopkins, 1994).

No Level 5 results were found for chimpanzees.

Overall, chimpanzees were largely unlateralized (Level 1), at least when observed ethologically while engaged in spontaneous, species-typical acts, so long as these tasks did not involve tools or more demanding, induced activities. The rightward shift for tasks in which both hands manipulated objects but each in different ways is notable (Hopkins, 1996), for this is not a frequent pattern in nature, except when eating (Marchant and McGrew, 1996). Similarly, the increase (from Level 2 to Level 4) in population-level bias caused by postural reconfiguration to assisted tripedality differs from that seen in other primates (cf. capuchin monkeys, Anderson et al., 1996; squirrel monkeys, Laska, 1996a), who went only from Level 1 to Level 2.

CONCLUSIONS

The biggest, simplest conclusion is that there is yet no compelling evidence that nonhuman primates are lateralized at the population level. That is, neither Level 4 nor Level 5 is the norm for any species, task, or setting, much less in one consensual direction, i.e. Level 4a and 5a vs. Level 4b and 5b. Instead, apart from the special case of chimpanzees (Table 6), all of the Level 4 findings in Tables 2–5 look tentative. For example, it may be that hands using tactile stimuli are lateralized to the left, and so reflect a right-hemisphere cerebral dominance or specialization (e.g. Fagot et al., 1991; Parr et al., 1997), but that remains to be established.

As for *Pan troglodytes*, even if the Level 4b findings are impressive (Hopkins 1993, 1994), they represent but a fraction of the species repertoire, and more importantly, there are discrepancies between findings from nature and from captivity. While captive chimpanzees tend to eat from the right hand, while holding food in reserve in the left hand (Hopkins, 1994), wild chimpanzees tend to eat equally often from left or right hand, whether or not the other hand is

holding food (Marchant and McGrew, 1996, Table 12). Put another way, the most common combination (approx. 60%) of bouts of eating at Gombe is for one hand to take food to the mouth while the other hand holds additional food, but the ratio of L:R for the other hand is still 50:50, whether or not the noneating hand is idle. For upright postures of assisted tripedality, the effect in captive chimpanzees is striking, especially given the large sample size of subjects (Hopkins, 1993). However, such postures are anomalous. Hunt (1996, Table 5) recently reviewed 15 studies of anthropoid posture, including four of chimpanzees. Bipedality was rarely seen in all of the data-sets and for chimpanzees, the highest frequency was 0.4% of the time. Why a quadrupedal primate should be more lateralized to the right when it is induced to stand upright is an intriguing question. Hunt (1996) hypothesized that upright posture for small-fruit harvesting may have been the kicking-off point for the evolution of hominid bipedalism, but he made no mention of laterality of function.

If population-level lateralization has not been shown to be characteristic of nonhuman primates, then it does not have to be explained. The unlateralized findings reviewed here in Tables 2–6 refute MacNeilage's (1987) "postural origins" theory, at least as applied to the whole order Primates. The data reviewed here also address more specific claims: MacNeilage et al. (1991, p. 344) stated that gorillas showed "... a significant humanlike pattern consisting of a greater number of animals which preferred the right hand *for all acts...*" (italics in original). Table 5 shows this clearly not to be the case (see also McGrew and Marchant, 1993).

Warren's (1980, 1987) view that nonhuman primates are essentially unlateralized, except by the distorting experiences of human influence, is now difficult to maintain. It is refuted by the increasing number of non-Level 1 findings from natural populations, where human elicitation of such patterns is hard to imagine, especially in non-provisioned populations (Byrne and Byrne, 1991, 1993; Boesch, 1991). Gombe's chimpanzees are lateralized at Level 3 for tool use in termite fishing, yet they have never seen a

human being perform the act (McGrew and Marchant, 1996). Finally, early lateralization of behavior in very young primates (neonatal chimpanzees, Bard et al., 1990; Fagot and Bard, 1995; Hopkins and Bard, 1993 a,b, 1995) makes it unlikely that extrinsic factors are the cause of this lateralization.

Fagot and Vauclair's (1991) dichotomous view of low-level and high-level tasks is better supported by the collective data of Tables 2–6. The basic act of simple reaching (see MacNeilage et al., 1987), that is, to extend the arm, grasp a food-item in the hand, and then flex the arm, is most commonly seen at Levels 1 and 2, as symmetrical as a low-level task should be, in their terms. However, high-level tasks, such as gorilla food processing (Byrne and Byrne, 1993) and chimpanzee tool use (Boesch, 1991, Sugiyama et al., 1993) are equally symmetrical at Levels 2 and 3. If novelty, and not cognitive or motor complexity, is the key to high-level tasks, then one must account for newly presented experimental tasks that still elicit individually (and not group-level) lateralized responses (Anderson et al., 1996; Parr et al., 1997; Rigamonti et al., 1997). It seems likely that the confounded components of Fagot and Vauclair's (1991) framework need to be systematically disconnected and tested, or the gradations between low- and high-level tasks made clearer, or both.

Thus, no existing theoretical framework seems able to explain the data on hand laterality as now accumulated.

Conspicuously absent from all the tables is any substantial evidence of human-like laterality of hand function, that is, performance at Level 5b. Only chimpanzees, with some manifestations of Level 4b (Hopkins, 1993, 1994) seem even close to resembling *Homo sapiens's* bias to the right. If there is nothing yet shown (e.g. by replication) in the natural behavioral repertoire of nonhuman primates that will allow us to model our own peculiar hand laterality, then we may well have to be content with the unnatural, that is, only by "humanizing" our relations in the controlled conditions of captivity may we be able to mimic the self-domestication of the hominid line in the evolutionary past (cf.

Hopkins, 1996). If our human handedness is unique, then we may seek its recent roots as an exaptation, perhaps to cortical lateralization for language, rather than as an ancient adaptation. In brief, the current evidence from our nonhuman primate relations suggests that laterality of hand preference in *Homo sapiens* is a highly derived characteristic.

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